BIONOMICS OF A SUBTERRANEAN GALL MIDGE (DIPTERA: CECIDOMYIIDAE) FROM *ARTEMISIA LUDOVICIANA*[1]

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Abstract.— Bionomics of a gall midge that emerged from nodulelike structures of herbaceous sage, *Artemisia ludoviciana*, was studied as a part of a larger investigation on possible nitrogen fixation by this plant. Infested plants collected from the field were regularly examined in the laboratory where some of them were grown in a liquid nutrient medium. In the laboratory, adult midges were reared from pupae and induction of infestation was attempted. Apparent nodulation of these plants is caused by the subterranean bud galls of a previously unknown gall midge, *Rhopalomyia subhumilis* Gagné. Life history of this midge is reported. These midges have one generation per year in the study areas and overwinter as larvae. There were no indications of paedogenesis. These midges are parasitized by a species of Platygasteridae.

Apparent nodulation on the underground parts of an herbaceous sagebrush, *Artemisia ludoviciana* Nutt., was reported by Farnsworth and Hammond (1968) in their investigations on nitrogen fixation by nonleguminous plants. Later, nitrogenase activity, measured through acetylene-ethylene gas assay, was recorded from these nodulelike structures (Farnsworth and Clawson 1972). When midges emerged from the stored mature bodies in the laboratory, it was hypothesized that they might act as vectors of the nitrogen-fixing microorganisms (Farnsworth 1975). It was also possible that the presumptive nodules actually were subterranean galls of a hitherto unknown midge that infested these plants. This study was undertaken to investigate the bionomics of these midges in relation to the nodulelike structures of these sage plants, as a part of a larger investigation of possible nitrogen fixation by *Artemisia ludoviciana*.

The midge that emerged from the nodulelike structures was found to be *Rhopalomyia subhumilis* Gagné, a species previously unknown to science, in the family Cecidomyiidae (Gagné 1977). This large family includes most of the economically important gall midges (Mani 1964). *Rhopalomyia subhumilis* is the only subterranean gall midge reported from *Artemisia*. It is one of the few gall midges known to inhabit the subterranean parts of the host plant.

Artemisia ludoviciana is an herbaceous plant with a perennial, subterranean, rhizomal stem. In Utah, the annual aerial growth of this plant persists from early spring to early fall. This plant is indigenous to much of the United States from western Canada and California eastward to Montana and the Dakotas.

The objective of the present research is to study the life history of this gall midge in relation to the galls of the host plant.

Rubsaamen (1892) erected the cosmopolitan genus *Rhopalomyia* which now contains over 200 known species (Gagné 1974), 56 of which are from North America north of Mexico (Foote 1965). Jones (1971) apparently found an additional 35 species from the *Artemisia tridentata* complex in Idaho, and in relation to this work Gagné (1974) revised the subgenus *Diathronomyia*. Gagné (1975) recognized additional new *Rhopa-*

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lomyia species. He has named and reviewed the taxonomic status of the gall midge reported in this paper (Gagné 1977).

Rhopalomyia species are apparently host specific and they are responsible for a particular kind of gall on some part or parts of the plant (Gagné 1974). Mani (1964) reported that galls of *Rhopalomyia* are largely confined to the Compositae, but a few make galls in plants belonging to other families (Felt 1940). Several *Artemisia* species harbor galls of *Rhopalomyia* (Felt 1940), although none has been reported from *Artemisia ludoviciana*. Most *Rhopalomyia* species show marked preference to flower and bud galls (Felt 1915). *Rhopalomyia thompsoni* Felt was named from the root galls of *Solidago rugosa* (Felt 1907), and *Rhopalomyia hirtipes* O.S. from both aerial and subterranean bud galls of *Solidago juncea* (Felt 1915). Published records of subterranean galls on *Artemisia* were not found, although galls are known to occur on other parts of these plants (Felt 1911b, 1940).

Earlier work on *Rhopalomyia* was mostly confined to records of rearing them from galls and to taxonomic descriptions (Felt 1907, 1911a, 1916). Cockerell (1909) described the biology of *Rhopalomyia betheliana* Ckll. from *Artemisia frigida*, and Lander (1951) reported a short description of an unidentified *Rhopalomyia* species from *Artemisia tridentata* Nutt., in Utah. The ecology of several apparent species of *Rhopalomyia* found on *Artemisia tridentata* complex in Idaho was studied by Jones (1971), and the biology of *Rhopalomyia hirtipes* from *Solidago juncea* was reported in detail by Spence (1969).

Materials and Methods

The study areas are located in the Manti-La Sal National Forest within an elevation range of 2,440 to 3,200 m and between 22 to 30 km southeast of Ephraim, Sanpete County, Utah, where an abundance of host material was available. This study was carried out from May 1976 to June 1977.

In the laboratory, for each gall the location on the host plant was recorded and the diameter was measured using a vernier caliper. Some of the galls were dissected under a stereoscopic microscope to record the number and stage of development of the midges found inside. An ocular micrometer was used for all linear measurements of the gall midges.

The soil-free, infested plants, supported by cotton wads kept on either side of the gallbearing section, were grown in glass tubes (Fig. 1) containing White's liquid nutrient medium (Paul 1970). Each tube was covered with black paper to prevent light penetration.

Adult midges were obtained from the mature galls by keeping them in plastic bags. Once emerged, the adult males and females were separated, their dimensions were recorded, and the midges were preserved in 70 percent alcohol. The adult parasites collected were also preserved in 70 percent alcohol.

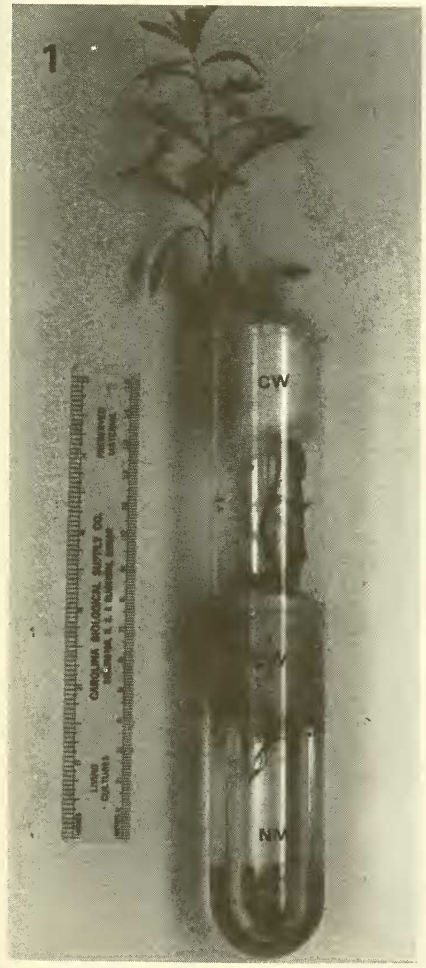
To find whether both the male and female midges emerged from the same gall, 24 mature galls were kept, each in a separate plastic vial (8.0 x 2.5 cm), between cotton wads at the top and the bottom of the vial. Some infested plants were kept intact in rearing chambers (36 x 26 x 26 cm), modified from Spence (1969), to allow observance of the adult behavior (Fig. 2). Some other infested plants were grown in a growth chamber at 35° C and 12 hours of daylight using White's liquid nutrient medium. Induction of the galls in the laboratory was attempted by keeping 24 uninfested plants in one half of a Plexiglas cage with a nylon-mesh-covered window, separated by a removable Plexiglas partition from the other half of the cage containing 24 infested plants (Fig. 3). These plants were grown in plastic trays containing cotton pads moistened with the liquid nutrient medium periodically. The partition was removed once the adult midges emerged and the uninfested plants were exposed to them. Later, these plants were examined for the signs of gall formation.

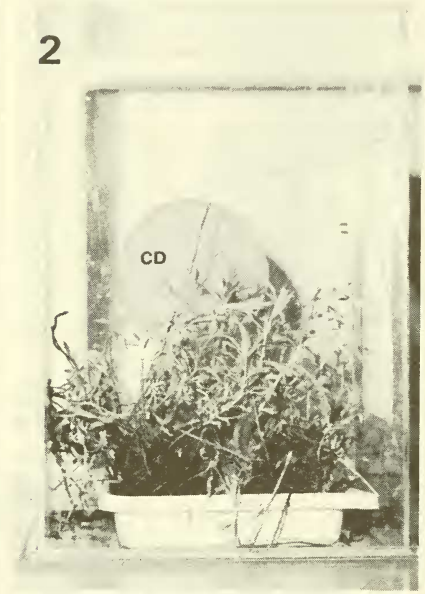
The photographs were taken using a Honeywell Pentax ® SP 1,000 camera, Vivitar extension tubes, and a Nikon ® stereoscopic microscope with the use of Panatomic ® X or Plux X ® films.

Results

Life History

Egg.— The eggs were first observed in the laboratory on 17 June 1976 but were collected from the field from 24 June to 17





Figs. 1-3: 1, Glass rearing tube with an *Artemisia ludoviciana* plant, CW-Cotton wad, NM-Nutrient medium. 2, Single-compartment midge-rearing cage, CD-Cage door. 3, Twin-compartment midge-rearing cage, CD-Cage door.

July 1976. These eggs were normally found in or near the leaf axils of the lower part of the aerial shoots and rarely on the underside of the leaves. In the laboratory the eggs were found even on the walls of the glass rearing tubes. Eggs were usually found in clusters varying from 12 to 49 eggs per cluster. Nine egg clusters included a total of 205 or an average of 23 eggs per cluster.

The eggs were pale red in color. The average measurements of 45 randomly selected eggs were 0.30 x 0.06 mm. Each egg was cylindrical in shape with tapering ends (Fig. 4). Under laboratory conditions the eggs hatched in three days at room temperature to produce pale red-colored, first instar larvae. In the field the exact time of hatching could not be determined, but on one occasion eggs observed in the field on 7 July at Skyline Drive could not be found during the next visit a week later, indicating that the eggs most likely hatched in less than a week.

Larva.— Earliest laboratory observation of the pale red-colored, first instar larvae was on 19 June 1976. Average measurements of 23 such larvae were 0.27 x 0.06 mm. When examined under the microscope, these larvae were found to crawl on the stem. However, the first instar larvae soon perished under laboratory conditions. In the field similar larvae were recovered from around the basal axillary buds of the shoots. On one occasion discarded pale red-colored larval skins were observed near a newly formed gall.

The first larva to be recovered from a new young gall was found on 8 July 1976 at the Blue Bell area at an elevation of 2,700 m when the soil temperature at a depth of 7 cm was 18° C. These larvae were colorless and translucent. Each of these larvae was confined to a distally tapering larval chamber which was slightly larger than the larva. The average of 33 such larvae measured was 0.35 x 0.23 mm. The midge overwintered in this larval form.

In the following spring few larvae similar to above were still found in the galls on 9 May 1977 at the Blue Bell area, soon after snow had melted. At Skyline Drive (elevation 3,300 m) these young larvae occurred even in the first week of June. At the Blue Bell area these young larvae were inside thin-walled, liquid-containing larval chambers of the galls located at the bases of aerial shoots about 1.7 cm high, growing in soil where the temperature at a depth of 2.5 cm was 8° C. However, by this time some larvae had already begun to develop (Fig. 5).

With the growth of the larva, the size and the wall thickness of the larval chamber increased progressively. But the distal end of the larval chamber remained comparatively thin walled and was oriented away from the basal attachment of the gall to the host plant. The fluid content of the larval chamber gradually decreased with the growth of the larva. No solid materials were found in the larval chambers at any time.

In the laboratory the young, growing larvae kept between the moist filter papers survived only up to three days, probably due to lack of nutrients. Hence the development of a given larva could not be followed through all the different stages by rearing them in the laboratory. Instead, midge galls regularly collected from the field during the growing season were dissected to follow the development of the larvae.

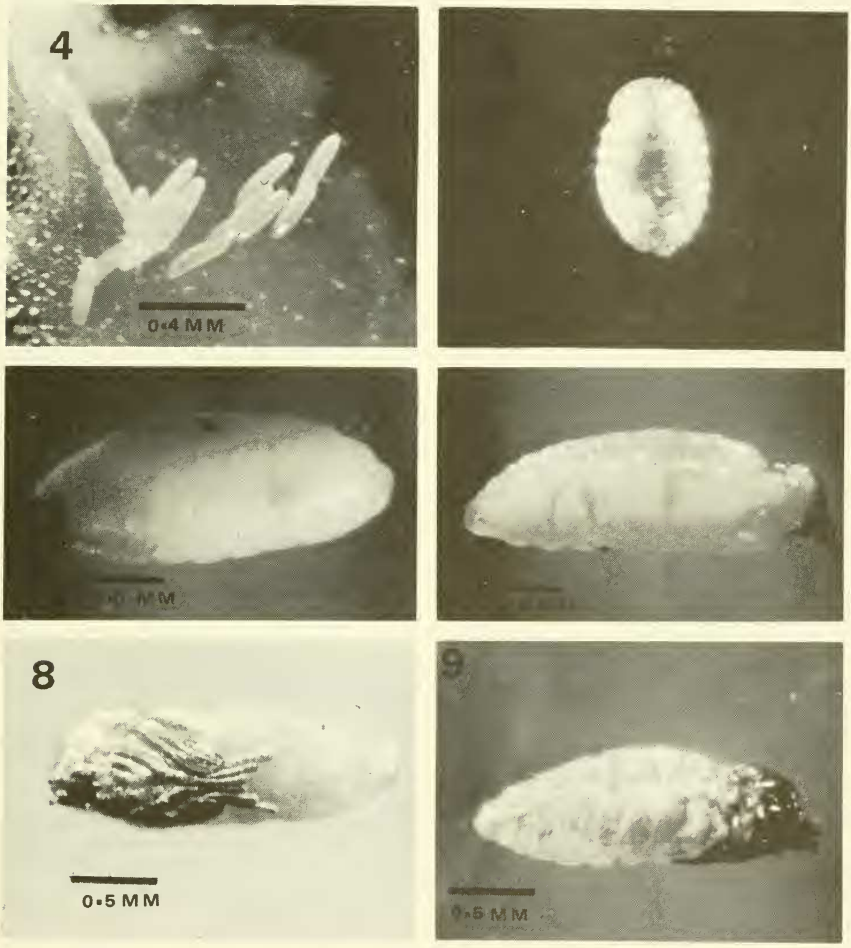
The range and the average of the lengths of the larvae collected from the field during their growing season are shown in Table 1.

Table 1. Larval lengths of *Rhopalomyia subhumilis* from *Artemisia ludoviciana* galls at Philadelphia Flat (1976).

Date	Number of larvae	Length in mm	
		Average	Range
03-VI-76	26	0.54	0.42-1.32
08-VI-76	47	0.78	0.42-1.38
17-VI-76	26	1.30	0.62-2.12
24-VI-76			
26-VI-76	17	1.51	0.81-2.12
01-VII-76	07	1.47	1.00-1.70
09-VII-76	15	1.56	*0.40-2.10

*New young larvae

During this period the length-to-width ratio of the larvae remained about 2:1. The largest larva observed was 2.12 x 1.00 mm. With growth, the originally colorless larva in the young gall changed to white, then yellow, and finally to brownish yellow at maturity. This mature larva (Fig. 6) was opaque compared to the translucent young larva. These midge larvae were rather characterless. The larval body consisted of 13 segments. The head capsule of the young larva was inconspicuous but became more



Figs. 4-9. Developmental stages of *Rhopalomyia subhumilis:* 4, Eggs. 5, Young larva. 6, Lateral view of the mature larva. 7, Lateral view of early pupa. 8, Ventrolateral view of late pupa. 9, Lateral view of female pupa just prior to eclosion.

visible with growth, due to pigmentation. The growing larvae were orientated with their heads toward the bases of the larval chambers until they reached the prepupal stage when their position reversed. The larvae were usually sluggish except for their feeding movements. When kept on a drop of water and subjected to intense light from a microscope lamp they moved away from the light by waves of body contractions.

Pupa.— The appearance of a pair each of antennal and facial horns on the ventral side at the anterior end of the mature larva was the first externally visible sign of pupation. At this time some of the other pupal structures were also visible through the cuticle of the prepupa. The horns were first visible on the laboratory-reared larvae on 9 June 1976, and the pupae were collected at Philadelphia Flat (elevation 2,900 m) on 15 June 1976.

This early pupa was white in color with a slight dorsal curvature of the body at the anterior end (Fig. 7). By the end of the first 24 hours the distal spines of the antennal and facial horns became brown in color, due to pigmentation. The compound eyes, which were white in color, became progressively browner within the first 48 hours, beginning around the ommatidia. On the fourth day a black bar appeared connecting the two eyes on the dorsal side. The eyes became black in color by the end of the fifth day. The pigmentation of the antennae commenced at their distal ends by the third day and then gradually proceeded toward the bases, making the orange-colored antennae entirely black by the end of the fifth day.

The white-colored thorax turned yellow within the first 24 hours and brownish red by the end of the third day. It became brown in color by the end of the fifth day, and by then two black bands appeared dorsolaterally at the posterior end of the thorax. The black coloration of the wing buds and the legs was initiated at their distal ends by the end of the third day and then gradually proceeded proximally to make them entirely black by the end of the fifth day.

The color of the pupal abdomen changed from white to pale yellow within the first 24 hours. In the male pupae this color intensified and then turned yellowish brown in the mature condition. But in the female, pupae the color of the abdomen gradually changed to pale red by the third day and then increased in intensity to become dark red upon maturation. The pupae were completely mature by the end of the sixth day (Fig. 8). The setal bands of the adult were visible through the pupal case just before eclosion, and the ovipositor in the female pupa was apparent by this time (Fig. 9).

The average length of 10 randomly selected mature male pupae was 1.92 mm, and that of 10 female pupae selected at random was 2.11 mm. In addition to this size difference the female pupae could be distinguished from the male pupae by the red-colored abdomen and comparatively shorter legs which extended only up to the end of the fifth abdominal segment. In contrast, the male pupae had a yellowish-brown abdomen and longer legs, which extended up to the end of the seventh abdominal segment.

I was able to rear the pupae from the first day of pupation to the adult stage by keeping them between moist filter papers in petri dishes at room temperature. The first adult emerged in the laboratory on 16 June 1976. Duration of the pupal stage varied from six to seven days in the laboratory at room temperature. In the field, pupal exuvia were first observed on 24 June 1976 at the Blue Bell area when soil temperature was 18° C at a depth of 6.0 cm.

Adults.— Immediately prior to eclosion the mature pupa became periodically active with bending movements of the body. The first signal of eclosion was the appearance of a longitudinal split along the mid-dorsal line of the pupal thorax. This thoracic split widened, exposing the adult thorax, and the adult head protruded through it with the eyes followed by the bases of the antennae. The white-colored adult thorax, bearing four dorsal bands of hair, emerged with the prothoracic legs coming out next and the halteres becoming free before the wings

(Fig. 10). Once the head and thorax were free, the adult apparently paused for a few seconds and then vigorously wriggled to free the abdomen from the pupal case. During eclosion the shaking of the free parts of the body perhaps helped to draw the encased parts out of the pupal case. In the laboratory eclosion was completed in 11 minutes for this pupa which was reared in a petri dish. The examination of the pupal exuviae indicated a similar process of eclosion under the field conditions. The pupal exuviae remained protruding out of the cavities of the gall surface (Fig. 11).

The adults emerged in the laboratory on 16 June 1976. In the field adult emergence occurred from 24 June 1976 (lower elevations) to 17 July 1976 (higher elevations). Adults were collected until 5 August 1976 from the infested plants reared in a growth chamber. When these plants were allowed to continue inside the growth chamber, five more adults emerged from the galls on the new shoots; they presumably belonged to a second generation. But no second generation adults were collected from the field.

Laboratory observations on 106 adults gave a male to female sex ratio of 1:1.9. Twenty-five randomly selected males averaged 1.76 mm in length, within a range of 1.28 to 2.12 mm. For 25 randomly selected females the average length was 1.96 mm within a range of 1.54 to 2.30 mm. These measurements were taken from the anterior end of the head capsule to the end of the last abdominal segment, exclusive of the antennae and the terminalia. The adult male has a yellowish-brown abdomen, comparatively long legs and a short pair of claspers (Fig. 12). The female could be recognized by her shorter legs, broad, red-colored abdomen, and the long ovipositor (Fig. 13). A complete description of the adults is presented by Gagné (1977).

Gravid females isolated from the males did not oviposit even after three days, but when adults of both sexes were present together they laid the eggs during the first day after emergence. I did not observe the act of mating, but it presumably took place shortly after emergence and lasted for a brief period of time.

Prior to oviposition the female probed over the host plant, apparently to select a suitable site. During oviposition the female was found near a leaf axil with her ovipositor extended. The longitudinal axis of her body was orientated to make a narrow angle with the stem. The prothoracic legs grasped the stem and the other legs supported the body. The metathoracic legs were observed to shake vigorously at intervals. The ovipositor was inserted into the leaf axil and the abdomen contracted periodically, accompanied by the wriggling movements of the ovipositor. This oviposition lasted four minutes in the laboratory.

The adults were never observed to feed, and their mouth parts were vestigial. The males were very active on the first day after emergence and they flew rapidly. They became lethargic and died on the second day. The females usually walked over the host plants after emergence and invariably rested for a few hours underneath the leaves (Fig. 14). They did not fly as swiftly as the males, but were still active on the second day after emergence. The females lived up to three days in the laboratory.

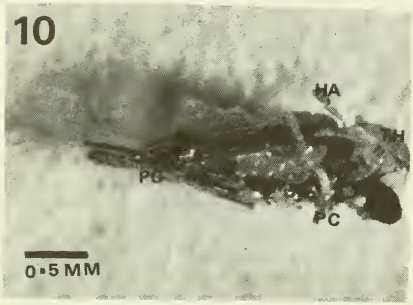
Parasites

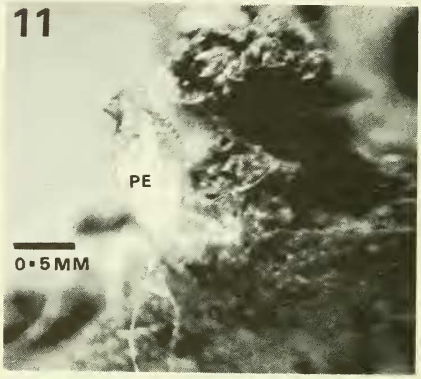
Twenty six of the 160 midge larvae, or 16.2 percent of the larvae examined, were parasitized by an undetermined species of Platygasteridae. However, this sample included 45 very young larvae, smaller than 0.5 mm, at which stage it was difficult to detect the presence of parasites. This parasite apparently laid its eggs on the midge eggs. The larvae of the parasite were first observed on 3 June 1976 when the host larvae had already begun their development in the larval chambers. I never observed more than one parasite per larval chamber. Either all of the larvae were found in a gall or only part of them were parasitized.

The larva of the parasite was invariably found on the midge larva. The earliest parasite larva observed inside a midge larval chamber measured 0.3 x 0.06 mm. It was

quite active compared to the lethargic midge larva and moved away from light. The host larva was not attacked until the parasite larva reached an advanced stage. The parasitized midge larvae were apparently more fragile and damaged easily during handling.

The parasite larva remained colorless up to its maturation, and just prior to pupation it bored into the midge larva near its anterior end. The first pupa of the parasite was observed on 30 June 1976. Six of these averaged 1.6 x 0.8 mm in dimensions (Fig. 15). The first adult parasite emerged on 18





Figs. 10-13: 10, Eclosion of the adult, HA-Haltere, PC-Pupal case, TH-Adult thorax. 11, Pupal exuvium protruding out of the gall surface, GA-Gall, PE-Pupal exuvium. 12, Lateral view of the adult female (ovipositor retracted). 13, Lateral view of the adult male.

June 1976 and they continued to emerge until 5 August 1976.

I did not observe any inquilines in the 77 galls dissected in the laboratory.

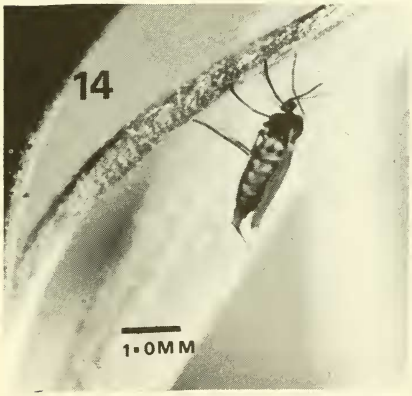
Galls

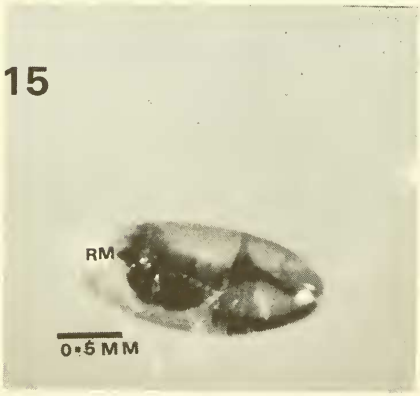
New galls were first observed in the field on 8 July 1976 at the Blue Bell area (elevation 2,700 m) in soil with a temperature of 18° C at a depth of 7.0 cm. The aerial shoots of most of the host plants were dying by this time, but a few young secondary shoots were still active. These young galls, covered by scale leaves, occurred at the bases of the dying aerial shoots and on the young rhizomal branches. Superficially, these appeared very similar to the axillary buds.

The galls remained dormant through the fall and winter months to resume their growth the following spring. On 9 May 1977 most of the galls were already growing at Blue Bell in soil at 8° C in temperature and at a depth of 2.5 cm. The spring growth of the galls and the host plants was concommitant till the galls reached maturity by the time of pupation of the midge, beginning early in June. The adults emerged as soon as the galls began to wither and dry, by late June (Fig. 16). Some of the old galls still remained attached to the host plant even in the following year.

The galls were confined either to the bases of the aerial shoots (Fig. 17) or to the active young branches of the rhizome (Fig. 18). No galls were found on the lateral roots (Fig. 18) or on the old rhizome. On the shoots the galls were largely restricted to the basal subterranean areas, but a few were also found protruding just above the soil surface. The depth of the galls in soil varied, depending on the soil texture. In decaying organic matter the galls were closer to the surface than in the loose loamy soil where they were down to a depth of about 4.0 cm.

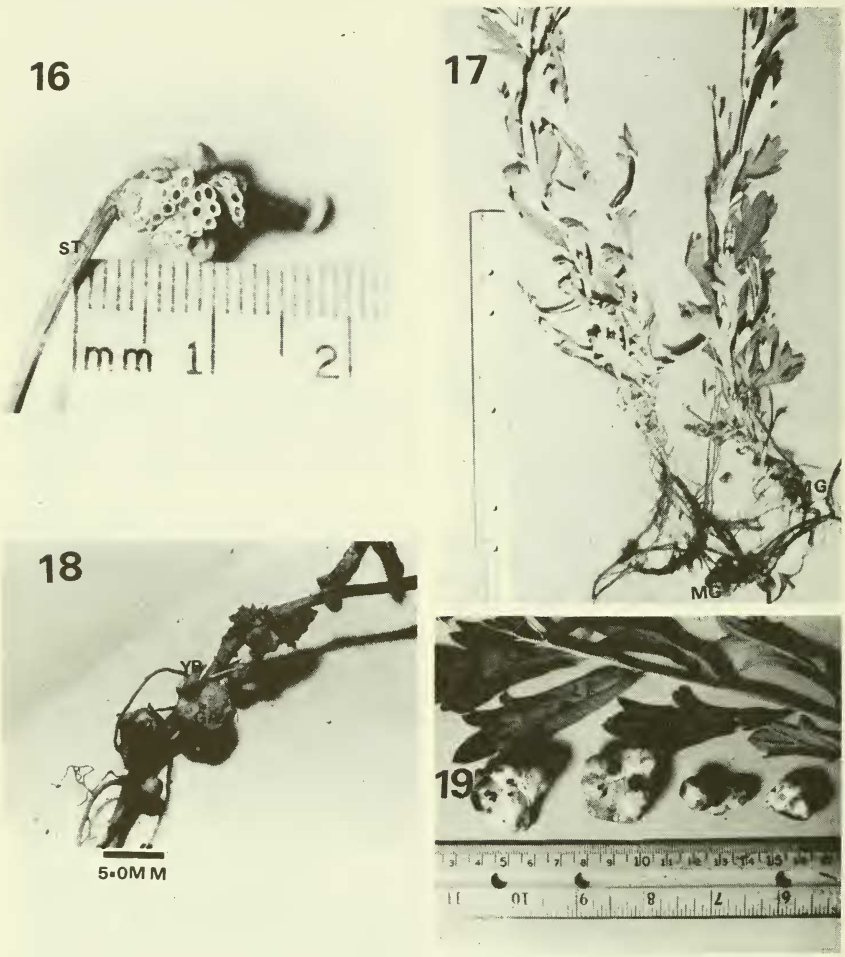
Out of a total of 77 galls examined in the laboratory, 32 (45 percent) were monothalamous and the remaining 45 (55 percent) were polythalamous. Galls occurred either singly or in clusters (Fig. 19). Single galls were more or less globose and the largest single gall measured 8.5 mm in diameter. The largest cluster of galls reached 25.0 mm across. These galls were creamy white in color, but a few had violet-colored areas on them during the early stages of growth. The galls exposed to sunlight developed a green color in the outer tissues.





Figs. 14-15: 14, Adult female resting underneath a leaf, LE-Leaf. 15, Pupa of the parasite, RM-Remnant of the midge larva.

The gall tissues initially consisted of moist, turgid cells which became dry after the maturation of the gall. In the polythalamous galls there was only one larva per larval chamber. In a given gall all the midges were in about the same stage of development. However, different galls, even those found on the same host plant simulta-



Figs. 16-19: 16, Partly dissected midge gall after the emergence of the adults, ST-Stem. 17, *Artemisia ludoviciana* plant bearing midge galls, MG-Midge galls. 18, Young rhizomal branch of *Artemisia ludoviciana* bearing galls, GA-Gall, YB-Young axillary bud. (Note absence of galls on lateral roots.) 19, Clusters of subterranean bud galls of *Rhopalomyia subhumilis* from *Artemisia ludoviciana*, LE-Close view of the host plant leaf.

neously, contained midges growing in different stages. The regression coefficient for the relationship between the size of the mature galls and the number of midges per gall is highly significant. This relationship is shown in Figure 20.

Out of the 24 galls kept individually in the plastic vials, only female adult midges emerged from seven galls, only male adults from three galls and both male and female adults emerged from two galls. From five other galls only adult parasites emerged. Both female adult midges and adult parasites emerged from two galls, and none emerged from the remaining five galls.

The attempt to induce gall formation by exposing uninfested plants to the newly emerged midges in the laboratory was not successful. However, when a number of infested host plants were allowed to grow inside a growth chamber, new galls were observed on the new shoots on 2 September 1976 and adults, possibly belonging to a second generation, were collected from these galls on 22 October 1976.

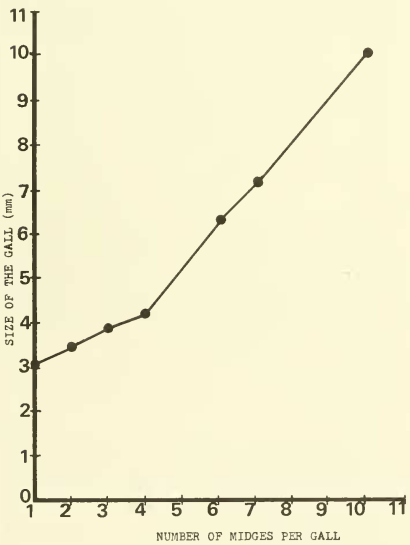


Fig. 20. Relationship between the number of midges per gall and the average size of the galls, (1976–77).

Discussion

These results indicate that the midge galls are modified axillary buds found either at the bases of the aerial shoots or on the new branches of the rhizome. Since only some of the aerial shoots and rhizomal branches had galls on them they are not likely to be the natural outgrowths of the host plants. On the contrary, the young galls and the axillary buds are so similar in appearance, it is not possible to distinguish between them without dissection under the microscope. Both the galls and the axillary buds are covered with scale leaves in the early stages of development and become activated about the same time in the spring. The spring and summer activation of the growth is characteristic of most of the other bud galls (Mani 1964). The absence of the galls either on the lateral roots or on the old rhizome, both of which are devoid of any active buds, further supports the view that these galls are modified buds. This view is also in accord with the preference of *Rhopalomyia* species for the bud galls (Felt 1915, 1940).

These growing buds may be preferred by the gall midges because they are well protected, readily supplied with the nutrients, and are in an active meristematic state—all of which are helpful for the formation of the galls (Felt 1936). Growing buds also may offer easily penetrable tissue for the young midge larvae. Subterranean buds in particular provide a microhabitat explored by relatively few other insects and apparently by none others in the case of *Artemisia*. The comparatively low rate of parasitism and apparent lack of inquilinism also indicate that subterranean galls could provide better protection for these midges.

The presence of the larvae of these midges in each and every gall dissected in the laboratory indicates that they may be the causative agents. The appearance of the galls in those buds close to the soil surface shows that they are caused by an aerial species (Mani 1964). Furthermore, the growth patterns of the galls and the midges are closely related. Although the laboratory induction of the galls by these midges was

not successful, their ability to induce galls was indicated by the emergence of a possible second generation of adults in October from those infested plants grown inside a growth chamber. The failure to induce galls was partly due to the asynchrony between the emergence patterns of the limited number of the adult males and females in the cage which resulted in their deaths without mating and the decaying of some of the galls brought from the field, probably due to their continuous contact with the nutrient medium. Attempts by Spence (1969) to induce galls of *Rhopalomyia hirtipes* in the laboratory also failed.

Association of bacterial and other types of microorganisms with the galls has been reported by others (Mani 1964). But the only report of bacterial microorganisms from *Rhopalomyia* galls is that by Farnsworth and Hammond (1968) for the galls of the midges under discussion. The attempts to find either the nitrogen-fixing bacteria by electron microscopy or to confirm the nitrogenase activity from these midge galls failed (Kent, unpublished data).

The eggs of these midges are laid in the leaf axils, which apparently provides them with shelter and protection from dessication. The female ovipositor is not adapted to lay the eggs into the host plant tissues and, consequently, eggs were never observed inside the host tissues. But the laying of some eggs on the wall of the glass tubes may be an indication of laying them on other inert surfaces like soil. But this was observed under the artificial conditions in the laboratory, and the eggs of this midge were never recovered from soil in the field. The eggs are comparatively smaller than in the related species and were visible to the unaided eye only when found in clusters. In the field the eggs were found over a period of three weeks, which apparently is responsible for the overlap of the different developmental stages.

The first stage larva was mobile and presumably induced the galls by invading the axillary buds. The exact mechanism of gall formation is not known. Since these young larvae lack well-developed mouth parts it is unlikely they bored into the host plant tissues. The passage of digestive enzymes from the larva to the gall tissues has been reported for other midge larvae (Bronner 1970), and it is possible for these midge larvae to secrete enzymes which could digest the host plant tissues, enabling them to enter the axillary buds. The larva is the sole trophic stage in the life cycle since the adults were never observed to feed. None of these midge larvae contained any smaller larvae inside them anytime, unlike in the case of the paedogenetic ones. Also, the adults of both sexes emerged from the same gall, which indicated again the lack of paedogenesis. Monothalamous galls are unlikely for the paedogenetic larvae, when only one larva is present in the mature state, as was found for these midges.

Inhabitants of a given gall were at about the same stage of development, which indicated the possibility of gall initiation by several larvae simultaneously. But even one larva is capable of gall initiation, as shown by the presence of the monothalamous galls. The young, first instar larvae presumably invaded the axillary buds at random. But since the number of axillary buds suitable for gall initiation would be limited at any given time, it is possible for the larvae from the same egg cluster to attack the same axillary bud and, therefore, to be found in about the same stage of development later. The size of a given gall was directly proportional to the number of midges found inside, which indicated a cumulative effect by the larvae which appeared to be the main influencing factor. The gall clusters may be the result either of multiple invasions by the young larvae at different intervals of time or an unusually large invasion by the young midge larvae on the same bud simultaneously.

As expected by the relatively long period of occurrence of the eggs in the field, different galls growing at the same time had larvae of different stages. The number of larval stages could not be determined, since the growing larvae did not survive outside the galls. But for most Cecidomyiidae, the

number of larval stages has been reported to be three (Gagné 1968).

Pupation occurred inside the galls as in most other *Rhopalomyia* species. The protrusion of the pupal exuviae perhaps facilitated the emergence of the newly hatched adult through the soil, although this has been observed for aerial species of midges as well (Spence 1969). This need for the adult to emerge through the soil imposes another restriction on the possible depth of the gall in soil. The vigorous preemergence movements of the pupa could help the passage of the pupal case containing the adult through the gall and soil under the field conditions.

The presence of some galls with adult midges belonging to one sex could be due to chance, since the females outnumber the males 2:1. Sex induction by the environment is another possibility, but no apparent relationship between the occurrence of this phenomenon and any one of the likely external factors could be found. Jones (1971) observed a similar relationship between the adult sex and the galls for a related midge species.

The short adult life span is common to most gall midges. This short life span, lack of feeding by the adults, and apparent need for mating prior to oviposition could all contribute to the need for quick oviposition and the localized pattern of infestation observed in the field. The sex ratio indicates the possibility of multiple matings for the male.

Apparently there is one generation of midges per year in the study areas since the eggs and the other developing stages were observed only in one continuous period during the year and the host plants had one relatively short growing season (Fig. 21).

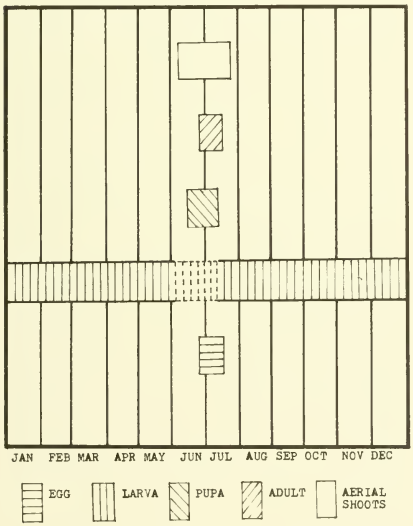


Fig. 21. Seasonal occurrence of *Rhopalomyia subhumilis* developmental stages and aerial shoots of *Artemisia ludoviciana* at Philadelphia Flat in 1976.

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